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CHARACTERIZATION OF *ANOPHELES PSEUDOPUNCTIPENNIS* LARVAL HABITATS

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ABSTRACT. A survey of *Anopheles pseudopunctipennis* larval habitats was performed throughout most of its known geographic range. Eleven key environment variables characterized most larval habitats of this important vector of malaria in the Americas. Larval habitats occurred mainly in valley and foothill areas which were often situated in arid regions. Immatures were found primarily during the dry season in sun-exposed freshwater stream pools with clear, shallow, stagnant water containing abundant filamentous green algae and/or aquatic vegetation.

INTRODUCTION

Anopheles (Anopheles) pseudopunctipennis Theobald is the most widely distributed anopheline mosquito in the New World (Rozeboom 1941). It is found from the southern USA (40°N) to the northern part of Argentina (30°S) along the Andes, with an eastern extension into Venezuela and the Lesser Antilles. It is the most important malaria vector in the foothills of mountainous areas of Mexico and Central and South America (Shannon and Davis 1927, Aitken 1945, Rodriguez and Loyola 1989). These areas correspond to some of the more remote and rugged malaria-endemic areas of North, Central, and South America. *Anopheles pseudopunctipennis* is often the only vector present in areas above 600 m and transmits malaria up to 2,800 m in Bolivia (Hackett 1945, Gorham et al. 1973). In the Americas, *An. pseudopunctipennis* is considered a major vector of malaria in 7 of 19 (37%) countries with endemic malaria (Pan American Health Organization 1994), including Argentina, Bolivia, Ecuador, Guatemala, Mexico, Nicaragua, and Peru.

Previous studies have described *An. pseudopunctipennis* larval habitats from different parts of the Americas, including Shannon and Davis (1927), Shannon (1930), Hoffmann (1931), Hoffmann and Samano (1938), Root and Andrews (1938), Aitken (1945), and Levi-Castillo (1945). In recent years, characteristics of *An. pseudopunctipennis* larval habitats also have been the subject of studies in Mexico and Belize (Savage et al. 1990; Rejmankova et al. 1991, 1993; Fernandez-Salas et al. 1994). However, comparison and characterization of *An. pseudopunctipennis* larval habitats from its entire known geographic range has not been accomplished prior to this study.

An extensive investigation of *An. pseudopunctipennis* along its neotropical distribution was undertaken in 1991 (Manguin et al. 1995); the characteristics of *An. pseudopunctipennis* larval habitats are summarized in this paper.

MATERIALS AND METHODS

Study area: Anopheles pseudopunctipennis was collected along its known geographic range and at altitudes from sea level up to 2,340 m. Ten countries (Table 1) were chosen according to critical locations, such as the type-locality of *An. pseudopunctipennis* in Grenada Island, and areas where 5 subspecies and one variant of this species were described (Knight and Stone 1977), and regions providing a spatial representation of the species' geographic distribution. In the Caribbean, *An. pseudopunctipennis* was sampled on Grenada Island. In North America, collections were made in the state of Texas and 2 areas of Mexico, Nuevo Leon (northeast) and Chiapas (southwest). In Central America, samples were taken in Belize and in 2 areas of Guatemala located along the drainage patterns of both the Pacific and Atlantic coasts. In South America, collections were made along the coastal plain and/or in the Andes in Chile, Colombia, Ecuador, Peru, and Argentina.

Mosquito collections: From 1991 to 1993, larvae and pupae of *An. pseudopunctipennis* were collected mainly along rivers and tributaries in the 10 countries listed above. The longitude and latitude of each habitat was recorded with a geographic positioning system (Ensign GPS). A standard data collection form developed by the Walter Reed Biosystematics Unit was used to record all the information necessary for our study, such as collection number, state, locality, date, time, type of collection, type of terrain and environment, and all the characteristics related to larval habitats. For all *Anopheles*-positive habitats, we recorded the type of larval habitat, water current, depth, shade, vegetation (submersed, floating, emergent), and algae

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Table 1. Geographic information on 60 *Anopheles pseudopunctipennis* larval habitats of 4 regions and 10 countries.

Region and country	State	Location	No. of samples
Caribbean			Subtotal: 3
Grenada	St. Patrick	Sallee River, Glassy River	3
North America			Subtotal: 8
USA	Texas	San Antonio: Fort Sam Houston (Area 9)	2
Mexico	Nuevo Leon	Monterrey: El Carmen, El Rancho del TEC	2
	Chiapas	Tapachula, Coatan River: El Plan, El Retiro, La Ceiba	3
	Chiapas	Zanatenco River: Tonalá	1
Central America			Subtotal: 22
Guatemala	Escuintla	Escuintla: Guachipilin, Maria Santissima	2
	Zacapa	Usumatlan: La Palmilla	1
	El Progreso	Guastatoya: Barrial, Morazan: Las Pericas	2
	Baja Verapaz	San Julian: El Patal	1
	Alta Verapaz	Tactic, Cobán: El Cruce	2
Belize	Cayo	Caves Branch, Sibun River, Silver Creek	11
	Cayo	Rio On	2
	Stann Creek	North Stann Creek	1
South America			Subtotal: 27
Colombia	Valle	Florida	2
Ecuador	Imbabura	Salinas	1
	Pichincha	Quito: Tumbaco	1
	Guayas	Guayaquil: Bucay, El Triunfo	3
Peru	Lima	Hacienda Villa, Rio Chillon	4
	Lima	Huachipa, Cieneguilla	3
	Cuzco	Quillabamba	1
Chile	Tarapacá	Arica: Rio Lluta, km25, km30, km35, km41, km53	6
	Tarapacá	Rio Azapa	1
Argentina	Salta	Puente Polares, Alemania, Santa Barbara	3
	Tucumán	Rio Tapia, Rio Vipos	2

(green, blue-green, filamentous, red). The aquatic plants were sampled and identified in the laboratory, and pH and conductivity were measured *in situ* with portable meters.

At each larval habitat, a minimum of 10 dips for anopheline mosquitoes was taken. All larvae or pupae were reared individually in vials and fed with fish food until pupation and adult emergence for identification. Anopheline adults were identified to species using Wilkerson et al. (1990), and associated fourth instar larval and pupal skins were preserved. Taxonomic voucher specimens have been deposited at the Walter Reed Biosystematics Unit of the Smithsonian Institution, Washington, DC.

RESULTS

The following results refer only to *An. pseudopunctipennis* larvae. Data on larval habitats are based on 60 positive collection sites located in 10 different countries (Table 1). The number of collecting sites by region varied from 3 in the Caribbean, where one country was sampled, to 27 in South America, where collections were made in 5 countries.

Types of environment, terrain and larval habitat (Table 2): Of 60 larval collections, 40% were made in relatively dry environments occurring in 7 of 10 sampled countries. In 5 countries, 27% of larval sites were located on agricultural land, such as orange groves, pastures, banana plantations, coffee plantations, and cultivated fields. Environments classified as forests (evergreen, coniferous, and cloud) were encountered in 3 countries. Finally, larval habitats also were found near villages, swampy areas, and prairies.

Larval habitats were encountered in 4 types of terrain. Valleys and foothills were the most common, with a frequency of 52 and 38%, respectively. Larvae also were collected in 4 sites along the coastal plain of Grenada and Peru, and from 2 sites along the Andean plateau of Argentina and Ecuador.

Half of the larval habitats were defined as stream pools, often with rocky bottom, or, in 23% of the cases, as stream margins. However, larvae were collected occasionally in other types of larval habitats, such as spring-seepages, ditches, ground pools, lagoons, and rock pools.

Color and depth of water (Table 3): Water was clear in 54 of the 60 positive larval habitats. Only 4 habitats had colored water, and 2 had turbid water. In one case, the turbidity was caused by con-

Table 1. Extended.

Elevation (m)	Longitude/Latitude
6	12°12′–11′N/61°37W
214	29°25′N/98°30′W
400	25°29–55′N/100°11–21′W
400–480	14°47′–15°00′N/92°28′W
40	16°05′N/93°45′W
250–320	14°15′N/90°47′W
500	15°00′N/89°30′W
600	14°50′N/90°00W
1,400	15°15′N/90°30′W
1,500	15°20′N/90°20′W
60–80	17°06–10′N/88°36–43′W
480	17°59′N/88°58′W
80	17°02′N/88°32′W
1,010	3°20′N/76°12′W
1,880	0°30′N/78°10′W
2,340	0°17S/78°32′W
10	2°16′S/79°20–53′W
3–100	11°50′–12°15′S/76°50′–77°00′W
300–320	12°00–10′S/76°50′W
988	12°50′S/72°50′W
200–850	18°20′S/69°30′W
274	18°20–30′S/69°30–70°00′W
1,160–1,440	25°00–50′S/65°15′W
700–800	26°30–40′S/65°20′W

tamination with cow feces (Salinas, Ecuador) and in another case by a recent flood (Monterrey, Mexico).

Most larval habitats had shallow water with over 60% being less than 10 cm deep. The association of shallow water with rocky bottom increased the difficulty of dipping for larvae.

Types of water movement, water body and sun exposure (Table 3): Stagnant water in larval sites was predominant over moving water in all countries except Grenada where the current was slow in all 3 larval collections. Sixty percent of water bodies were temporary. A total of 88% of the sites were exposed to the sun, including 50% of heavy and 38% of partial presence of sunlight. Only 12% of the sites were fully shaded.

pH and conductivity (Table 4): Larvae were collected in water with wide pH values ranging from 4.5 to 8.8. Almost half of the sites had an acidic to neutral pH, with values ranging between 6.02 and 7.0. Only one larval site had a pH as low as 4.5 (Huachipa, Peru). The other half of the sites had an alkaline pH, including 16 habitats with a pH below 8.0 and 9 sites with a pH between 8.0 and 8.8.

Water conductivity values varied between 45 and 8,350 μS, but the majority of larval sites had freshwater with conductivity values lower than 650 μS. Brackish water was found in 10% of larval habitats (conductivity > 5,000 μS).

Altitude: Larvae were found from sea level up to 2,340 m, but the collections were mostly made at altitudes below 100 m (36%) and between 100 and 500 m (33%). Above 500 m, larval sites were not always accessible, and the frequency of sampling was reduced to 14% between 500 and 1,000 m and 15% between 1,000 and 2,000 m. Only one larval site, located in the Andes of Ecuador, was sampled above 2,000 m (Table 1).

Presence and absence of algae and vegetation (Table 5): In all 10 countries, larvae were highly associated with algae, with a frequency of 93%. Only 4 exceptions occurred, in Belize, Chile and 2 sites in Guatemala where no visible algae were present. In most collections, larvae were associated with mats of either green or filamentous green algae. Different types of green algae such as *Cladophora* and *Enteromorpha,* were found, but larvae were most commonly associated with the *Spirogyra*-type, a filamentous green alga.

Most larval sites had emergent, floating, and submersed vegetation. Emergent vegetation was most common. A mixture of these 3 categories of vegetation was also positively associated with the presence of larvae. No larvae were collected in habitats where both algae and vegetation were absent.

Associated anopheline species: Of the 60 larval collections of *An. pseudopunctipennis,* 40% contained larvae of other *Anopheles* species. In the Caribbean (Grenada), *An. pseudopunctipennis* larvae were sympatric with 2 *Anopheles* species (Manguin et al. 1993): *Anopheles aquasalis* Curry, occurring at sea level, and *Anopheles argyritarsis* Robineau-Desvoidy, a ubiquitous species in Grenada that was found in a wide range of altitudes (6–480 m). In North America, *An. pseudopunctipennis* larvae were collected in association with *Anopheles punctipennis* (Say) larvae in one of the 2 habitats sampled in Texas (USA). In Central America, *An. pseudopunctipennis* larvae were found in high-altitude habitats (1,400–1,500 m) with *Anopheles hectoris* Giaquinto-Mira in Guatemala, and in association with 3 species, including *Anopheles albimanus* Wiedemann, *An. argyritarsis,* and *Anopheles darlingi* Root, in Belize at elevations between 60 and 80 m. In South America, larvae of the *An. albimanus* Section were associated with *An. pseudopunctipennis* in 2 habitats in Argentina (700 and 1,160 m), one in Ecuador (10 m), and one in Peru (988 m). Larvae of the *An. argyritarsis* Section were collected with *An. pseudopunctipennis* in all 5 larval habitats sampled in Argentina (700–1,186 m) and one in Chile (847 m). Finally, larvae of *Anopheles punctimacula* Dyar and Knab and *An. pseudopunctipennis* were found in sympatry in one Ecuadorian habitat (10 m).

DISCUSSION

Our survey of *An. pseudopunctipennis* larval habitats throughout its geographic range confirmed

Table 2. Number and frequency of environment, terrain, and larval habitat types and country for positive *Anopheles pseudopunctipennis* larval collections.

	n	Frequency (%)	Country[1]
Environment			
Dry area			
1. Scrub	12	20	AR, ECU, GT, MX, PE, USA
2. Desert	12	20	AR, CH, MX, PE
Subtotal	24	40	
Plantation			
1. Orange grove	4	7	BHZ
2. Pasture	4	7	BHZ, GT
3. Banana plantation	3	5	ECU
4. Coffee plantation	3	5	MX
5. Cultivated field	2	3	COL
Subtotal	16	27	
Forest			
1. Evergreen forest	9	15	AR, BHZ, GT
2. Coniferous forest	1	2	BHZ
3. Cloud forest	1	2	GT
Subtotal	11	19	
Other			
1. Village	6	10	GR, MX, PE
2. Swamp	2	3	PE
3. Prairie	1	2	AR
Subtotal	9	15	
Terrain			
1. Valley	31	52	AR, BHZ, CH, COL, ECU, GT, MX, PE, USA
2. Foothill	23	38	AR, BHZ, CH, GR, GT, MX, PE
3. Coastal plain	4	7	GR, PE
4. Plateau	2	3	AR, ECU
Larval habitat			
1. Stream pool	30	50	AR, BHZ, CH, GT, MX, PE
2. Stream margin	14	23	BHZ, CH, GR, GT, PE
3. Spring-seepage	5	8	GT, PE, USA
4. Ditch	5	8	COL, ECU, USA
5. Ground pool	3	5	ECU, MX
6. Lagoon	2	3	BHZ, ECU
7. Rock pool	1	2	CH

[1] AR, Argentina; BHZ, Belize; CH, Chile; COL, Colombia; ECU, Ecuador; GR, Grenada; GT, Guatemala; MX, Mexico; PE, Peru; USA, United States.

the previous findings that larvae occur most frequently in freshwater stream pools with still, shallow, clean water and abundant filamentous green algae (Hoffmann 1927, 1931; Shannon 1930; Hoffmann and Samano 1938; Rozeboom 1941; Hackett 1945). Recent studies in Mexico and Belize on environmental associations of *An. pseudopunctipennis* larvae identified 3 principal positive variables: filamentous green algae, altitude, and shallow water (Savage et al. 1990; Rejmankova et al. 1991, 1993; Fernandez-Salas et al. 1994). In order to provide a more comprehensive characterization of *An. pseudopunctipennis* larval habitats, the present survey was conducted over most of the known geographic range of the species.

The majority of larval habitats were found in dry environments in valleys or foothills, confirming earlier findings that this species inhabits arid canyons and valleys where the immature forms find ideal conditions for growth in the small, slow-moving streams and side pools of receding rivers containing a rich growth of green algae (Shannon and Davis 1927, Shannon 1930, Aitken 1945). Larvae also are tolerant of water temperature fluctuations and drought (Gorham et al. 1973). Hoffmann (1931) defined *An. pseudopunctipennis* as a xerophile species with a peak abundance during the dry season. Seasonal rainfall has been reported to be negatively associated with larval abundance (Savage et al. 1990, Fernandez-Salas et al. 1994). Heavy rains cause rivers and tributaries to rise suddenly and transform into rapidly flowing waters. As a consequence, river pools containing filamentous algae and larvae are purged. In addition, water which becomes muddy is unsuitable for *An. pseudopunctipennis* larvae (Hoffmann 1931). The increase in numbers of pools in the riverbed was inversely related to rainfall, and it seems likely that with the

Table 3. Depth of water, types of water movements, water bodies, and sun exposure for positive *Anopheles pseudopunctipennis* larval collections with country association.

	n	Frequency (%)	Country[1]
Depth (d)			
d ≤ 5 cm	26	43	AR, BHZ, CH, ECU, GT, MX, PE
5 cm < d ≤ 10 cm	12	20	AR, BHZ, COL, GR, GT, MX, PE
10 cm < d ≤ 50 cm	10	17	BHZ, CH, ECU, MX, USA
50 cm < d ≤ 1 m	10	17	BHZ, CH, COL, ECU, GR, GT, PE
1 m < d ≤ 2 m	2	3	GT, USA
Range: 2 cm–2 m	60	100	
Water movement			
1. Stagnant	38	63	AR, BHZ, CH, COL, ECU, GT, MX, PE, USA
2. Slow	21	35	BHZ, CH, COL, GR, GT, PE, USA
3. Moderate	1	2	GT
Water body			
1. Temporary	36	60	AR, BHZ, CH, COL, ECU, GT, MX, PE, USA
2. Permanent	24	40	BHZ, CH, ECU, GR, GT, PE, USA
Sun exposure			
1. Heavy	30	50	AR, BHZ, CH, COL, ECU, GR, GT, MX, PE, USA
2. Partial	23	38	AR, BHZ, CH, COL, ECU, GR, GT, MX, PE
3. Absent	7	12	AR, BHZ, CH, ECU, GT, PE

[1] AR, Argentina; BHZ, Belize, CH, Chile; COL, Colombia; ECU, Ecuador; GR, Grenada; GT, Guatemala; MX, Mexico; PE, Peru; USA, United States.

sudden disappearance of preferred oviposition sites, females begin selecting rain pools as alternative sites (Fernandez-Salas et al. 1994).

Larval habitats were found in various environments, such as plantations, forests, villages, swamps, and prairies. While most larval habitats were associated with stream pools and stream margins, larvae were also found in spring-seepages, ditches, ground pools, lagoons, and rock pools (Table 2). Howard et al. (1917) characterized the association of *An. pseudopunctipennis* larvae with clean water. Larvae have also been reported from artificial containers, such as reservoirs, tanks, fountains, well-holes (Rozeboom 1941), rice paddies, and marshy meadows (Downs et al. 1948). Some of these unusual habitats had larvae only during the rainy season when females apparently oviposit in alternative habitats.

During our study, larvae were mainly collected in clear, shallow stream pools with rocky bottoms. A large majority of the sites were exposed to the sun, which is in agreement with earlier findings

Table 4. pH and conductivity of 48 positive *Anopheles pseudopunctipennis* larval collections.

	n	Frequency (%)	Country[1]
pH			
1. Acidic-neutral (4.5 ≤ pH ≤ 7.0)	23	48	BHZ, CH, ECU, GR, GT, PE
2. Alkaline (7.0 < pH ≤ 8.8)	25	52	AR, BHZ, CH, ECU, GR, GT, PE, USA
Range: 4.5–8.8	48	100	
Conductivity (C)			
1. Freshwater (c ≤ 650 μS)	27	56	AR, BHZ, ECU, GT, PE, USA
2. Slightly brackish (650 μS < c ≤ 2,000 μS)	8	17	AR, GR, PE, USA
3. Moderately brackish (2,000 μS < c ≤ 5,000 μS)	8	17	CH, GR
4. Brackish (c > 5,000 μS)	5	10	AR, ECU, GR, PE
Range: 45–8,350	48	100	

[1] AR, Argentina; BHZ, Belize; CH, Chile; COL, Colombia; ECU, Ecuador; GR, Grenada; GT, Guatemala; MX, Mexico; PE, Peru; USA, United States.

Table 5. Presence/absence on types of algae and vegetation for 60 positive *Anopheles pseudopunctipennis* larval collections.

	Frequency		
	n	(%)	Country[1]
Algae			
Absence	4	7	BHZ, CH, GT
Presence	56	93	AR, BHZ, CH, COL, ECU, GR, GT, MX, PE, USA
Type of algae			
1. Green	31	55	AR, BHZ, CH, COL, ECU, GR, GT, PE
2. Filamentous-green	21	37	BHZ, CH, ECU, GT, MX, PE, USA
3. Green and red	2	4	CH
4. Red	2	4	CH, USA
Vegetation			
Absence	14	23	AR, BHZ, GT, MX, PE, USA
Presence	46	77	AR, BHZ, CH, COL, ECU, GR, GT, MX, PE, USA
Type of vegetation			
1. Emergent	21	46	AR, CH, COL, ECU, GT, MX, PE
2. Floating	13	28	BHZ, ECU, GR, GT, USA
3. Submersed	1	2	GT
4. Floating and emergent	6	13	BHZ, ECU, GT
5. Submersed and floating	4	9	AR, BHZ, GR
6. Submersed and emergent	1	2	COL

[1] AR, Argentina; BHZ, Belize; CH, Chile; COL, Colombia; ECU, Ecuador; GR, Grenada; GT, Guatemala; MX, Mexico; PE, Peru, USA, United States.

(Shannon and Davis 1927, Rozeboom 1941, Hackett 1945). The development of algae is dependent on the presence of sunlight and *An. pseudopunctipennis* larvae are significantly ($P < 0.0001$) associated with the presence of green algae (Rejmankova et al. 1993); therefore, its larval habitats and sunlight are also associated.

Larvae were mostly collected in habitats with stagnant water; however, larvae also were found in flowing water where the presence of green algae seemed to drastically reduce water current velocity within the habitat. Larvae and pupae were often concentrated on top and inside of thick mats of filamentous green algae. Phytoecological relationships between *An. pseudopunctipennis* larvae and green-filamentous algae have been reported throughout the species' geographic distribution (Shannon and Davis 1927; Root and Andrews 1938; Aitken 1945; Hackett 1945; Savage et al. 1990; Rejmankova et al. 1991, 1993; Fernandez-Salas et al. 1994). Five genera of green algae were significantly associated with larval habitats: the most prevalent was *Spyrogira* (especially *S. malmeara* and *S. mayuscula*), followed by *Oedogonium, Chladophora, Closterium,* and *Enteromorpha.* The latter alga is known as an indicator of brackish water and was found in abundance in the Sallee River of Grenada Island (Manguin et al. 1993). *Spirogyra* algae form mats that provide not only shelter to *An. pseudopunctipennis* larvae, especially against predators and water current, but also food (Hoffmann and Samano 1938). It is not uncommon to collect larvae with a green color from feeding heavily on green algae. In most cases, abundant algal growth was a key factor for the presence of larvae. Fernandez-Salas et al. (1994) stated that in Mexico (Coatan River, Chiapas), *An. pseudopunctipennis* larval densities were positively associated with the percentage of surface area covered with filamentous algae ($P = 0.0001$). Range limits for mean numbers of larvae collected were 16.7–53.9 larvae per m^2 of filamentous algae (Fernandez-Salas et al. 1994). However, during our survey, larvae were also collected in habitats without any visible algae. In different localities, Hoffmann (1927) observed large quantities of larvae between stones and small sand bars of rivers, without the presence of noticeable vegetation, algae, or other aquatic flora. During our survey, larvae were never found in habitats without either algae or aquatic vegetation. Most larval habitats contained various vegetation types—emergent, floating, submersed, or a mixture of these different types. In river pools in southern Mexico, larvae have been positively associated with emergent vegetation such as *Ludwigia octovalvis, Panicum* spp., *Paspalum* spp., and *Cyperus* spp. (Fernandez-Salas et al. 1994), whereas in spring seepages, larvae have been associated with *Heteranthera limosa,* a semiaquatic plant, as well as floating leaves or plants common in ponds, such as a water hyacinth, *Eichhornia crassipes,* and a water lettuce, *Pistia stratiotes.* In Mexico, *Heteranthera reniformis* was associated with *An. pseudopunctipennis* larval habitats along stream margins and floodplain pools during the dry season (Savage et al. 1990). In Grenada, Root and Andrews (1938) observed larvae in floating mats of *Ceratophyllum.* In agreement with Rozeboom (1941), we found that *An. pseudopunctipennis* larvae move onto the upper surface and partially ad-

here to leaves or other floating vegetation. Emergent and floating vegetation, either macrophytes or microphytes, probably have direct or indirect roles in stimulating *An. pseudopunctipennis* females to select particular oviposition sites (Fernandez-Salas et al. 1994).

Larvae were collected in acidic, neutral, and alkaline water, with pH values ranging from 6.02 to 8.8. Only one site in Peru (Huachipa) had a pH as low as 4.5. In Ecuador, Levi-Castillo (1945) found the water of *An. pseudopunctipennis* larval sites to be alkaline with a pH ranging from 7.5 to 8.5. We found that most larval habitats contained freshwater with conductivities below 650 μS, but larvae were also found in slightly brackish, moderately brackish, and brackish water with a conductivity up to 8,350 μS. In the Sallee River on Grenada Island, where *An. pseudopunctipennis* larvae represented 99% of those collected, the river was fed by mineral springs rich in various salts which drastically increased the water conductivity (Manguin et al. 1993). In Peru, some larvae were collected in coastal plain habitats that were fed by seawater infiltration. In the Argentine and Ecuadorian Andes, larvae were found in high-elevation river pools (1,186 and 1,880 m, respectively) that were rich in salts.

During our survey, *An. pseudopunctipennis* larvae were collected from sea level up to 2,340 m in the Andes. In other studies, larvae were reported at elevations up to 2,300 m in Mexico, 2,800 m in Bolivia, and 3,200 m in Peru (Hoffmann 1931, Aitken 1945, Vargas and Martinez-Palacios 1956, Gorham et al. 1973). *Anopheles pseudopunctipennis* occurs at near the highest elevation from which malaria is endemic in the Western Hemisphere (Levi-Castillo 1945) and the world (Hackett 1945). However, *An. pseudopunctipennis* larvae are not restricted to high elevation habitats, but also occur at elevations as low as sea level.

Hackett (1945) stated that several other anophelines occurred with *An. pseudopunctipennis* over a considerable portion of its distribution. In our study, 2 subgenera (*Anopheles* and *Nyssorhynchus*) and 7 *Anopheles* species (*An.* [*Nys.*] *albimanus, An.* [*Nys.*] *aquasalis, An.* [*Nys.*] *argyritarsis, An.* [*Nys.*] *darlingi, An.* [*Ano.*] *hectoris, An.* [*Ano.*] *punctimacula, An.* [*Ano.*] *punctipennis*) and 2 *Anopheles* sections (*An. albimanus* and *An. argyritarsis* sections) were collected in association with *An. pseudopunctipennis.* These species associations changed from one geographical region to another in relation to the respective range of each species.

The status of *An. pseudopunctipennis* as a single species or a species complex is controversial (Estrada-Franco et al. 1992, 1993a, 1993b; Manguin et al. 1995; Munstermann 1995). If we allow for natural variation, the results of this survey show a remarkable consistency in the characteristics of *An. pseudopunctipennis* larval habitats from Texas to northern Argentina.

In conclusion, 11 key environment variables were found to be consistent for the majority of *An. pseudopunctipennis* larval habitats throughout its geographic distribution. We found that larval habitats of *An. pseudopunctipennis* mainly occurred in valleys and foothills which were frequently situated in dry environments. Larvae were found in sun-exposed freshwater stream pools containing abundant filamentous green algae and aquatic vegetation, with clear, shallow, and stagnant water. The highest population densities of this species occurred during the dry season. The association of these different variables with *An. pseudopunctipennis* larval habitats improves our knowledge of the species as well as aids in the development of potential strategies to control this important malaria vector.

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